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Can Thin-lipped Mullet Directly Exploit the Primary and Detritic Production of European Macrotidal Salt Marshes?

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Juveniles and adults (>100 mm) of *Liza ramada* colonize macrotidal salt marsh creeks of Mont Saint-Michel bay (France) between March and November, during spring tide floods (43% of the tides) and return to coastal waters during the ebb. This fish species actively feeds during its short stay in the creek (from 1 to 2 h). On average, each fish swallows sediment including living and inert organic matter, which amounts to 8% of its fresh body weight. Their diet is dominated by small benthic items (especially diatoms and salt marsh plant detritus), that correspond to the primary and detritic production of this macrotidal salt marsh creek. Despite very short submersion periods, mullets filter and ingest large quantities of sediment and concentrated organic matter (on average organic matter in stomach content is 31%) produced by these coastal wetlands. European salt marshes are thus shown to act as trophic areas for mullets, which are well adapted to this constraining habitat which is only flooded for short periods during spring tides.

Keywords: *Liza ramada*; tidal salt marsh; feeding; adaptation; organic matter fluxes

Introduction

North American salt marshes are known to play a trophic role for many fishes and macrocrustaceans (Shenker & Dean, 1979; Boesch & Turner, 1984; Kneib, 1997). Many of these species depend, for some period of their life cycle, on the intense primary productivity and refuge provided by vascular plants. Along the north East Coast of North America, the salt marshes occupy the major part of the intertidal area and are immersed at each tide (McKee & Patrick, 1988). In most European bays and estuaries, salt marshes are confined to the uppermost part of the intertidal area where they are immersed only periodically by spring high tides (Morley, 1973; Beeftink, 1977). Only few fish species invade this environment during the short period of submersion (Cattrijsse *et al.*, 1994; Laffaille *et al.*, 2000a; Mathieson *et al.*, 2000). Mulletts, especially *Liza ramada* (Risso, 1826), largely dominate this community and represent 87% of the biomass of the sampled fish community in the Mont Saint-Michel bay, France (Laffaille *et al.*, 2000a). This species is the

most abundant limno-benthofagous species both in tidal flats and estuaries in this coastal region of France (Feunteun & Laffaille, 1997; Laffaille *et al.*, 2000b).

Mulletts are among the most common species of tropical and temperate marine coastal waters in the world (Nelson, 1994) and constitute a fundamental protein resource for a number of human populations living in coastal areas. Thus, their biology and ecology have often been studied in numerous environments (Thomson, 1966; Zisman *et al.*, 1975; Collins, 1981; Al-Daham & Wahab, 1991). Although, an abundant literature focuses on various aspects of mulletts' feeding habits (Odum, 1968; Albertini-Berhault, 1974; De Silva & Wijeyaratne, 1977; De Silva & Silva, 1979; De Silva, 1980), the available literature concerning feeding ecology of *Liza ramada* focuses on young stages (Albertini-Berhault, 1973, 1974, 1979; Zismann *et al.*, 1975; Ferrari & Chierigato, 1981) or in fish farming systems (Yashouv & Ben-Sachar, 1967; Cardona & Castello, 1994; Cardona, 1996). Only Hickling (1970), Almeida *et al.* (1993), and Shapiro (1998) have studied the feeding habits of juveniles and adults in natural environments.

Compared to other marine, brackish and freshwater habitats, there are very few quantitative studies

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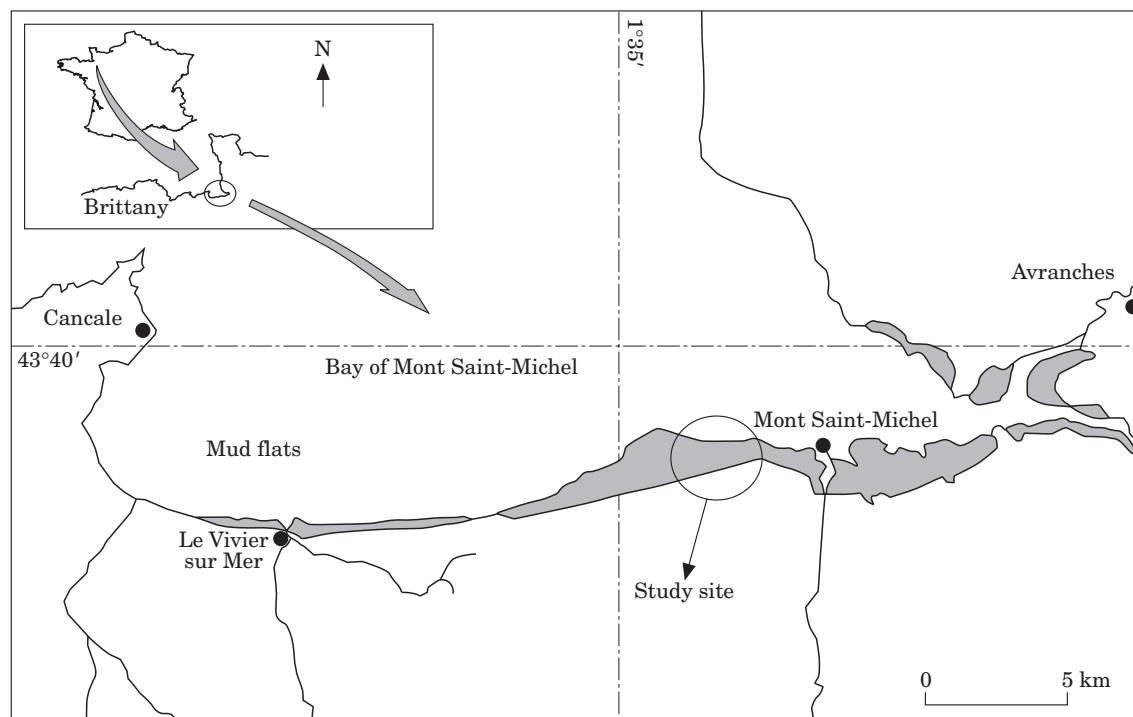


FIGURE 1. Location of the Mont Saint-Michel bay and study site.

concerning the feeding ecology of fish populations dwelling in these tidal wetlands, especially in Europe. Thus, the objective of this study is to describe the diet of juvenile and adult (>100 mm) *Liza ramada* mullets in the macrotidal salt marsh creek of the Mont Saint-Michel Bay in order to know if thin-lipped mullet can directly exploit the primary and detritic production of macrotidal salt marshes.

Material and methods

Study site

The Mont Saint-Michel bay (France) is a 500 km^2 littoral zone situated in the Normano-Breton Gulf (lat. $48^\circ40'N$, long. $1^\circ40'W$) (Figure 1). This bay is a semi-diurnal macrotidal system with the second highest tidal range in Europe (average: 10–11 m and up to 16 m). The intertidal zone covers 220 km^2 including 180 km^2 of mud flats and 40 km^2 of salt marshes.

The seawater goes into a dense network of creeks inside these salt marshes during a number of tidal cycles. The study site (Figure 1), located at the West of the Mont Saint-Michel and dominated by *Atriplex portulacoides* (Bouchard & Lefeuvre, 1996), is situated on a 15 m wide creek. The water only reaches this creek during 43% of the tides, when the water level is

higher than 11.25 m. Salt marsh vegetation is flooded only when tidal amplitudes are greater than 12.40 m (5–10% of tides). The creek is flooded on average for 2 h every springtime (Troccaz *et al.*, 1994). During the rest of the time, the salt marshes, including tidal creeks and vegetated tidal flats, remain unflooded.

Fish sampling

In this creek, *Liza ramada* were sampled during 50 high spring tides between January and December 1997. The sampling technique described by Laffaille *et al.* (1998) was applied. A fyke net (4 mm mesh size kуст to kуст, 5 m deep, 1.8 m high and 20 m long) and three trammel nets (30 to 70 mm mesh size kуст to kуст, 2 m high and 30 m long) were set across the creek. Each month, the mullets were caught during two different and consecutive tides during entire flood or ebb in order to analyse quantitatively and qualitatively the stomach contents before and after their residence in the salt marsh creeks. In each tide, nets remained in the creek for the entire flood or ebb period.

The fish lengths were measured to the closest mm (fork length, FL) and weighed to the nearest g (individual fresh body weight, BW). All the sampled mullets were deep-frozen (-18°C) until laboratory analyses.

Diets

The entire content of the digestive tract of each mullet was extracted and weighed to the nearest 0.1 g (gut content fresh weight, FW). The gonads were also weighed (GW). The instantaneous feeding ration (%Ir) was calculated according to Laffaille *et al.* (1999): $\%Ir = [FW/(BW-GW)] \times 100$. In all the cases, mullets colonized the marsh creeks with the flood and set out of the creeks with the ebb (Laffaille *et al.*, 2000a). Thus, the material (including organic and inorganic compounds) contained in the digestive tract of the fish captured during flood must have come from the adjacent mud flats; whereas those of the mullets captured during ebb came from the mud flats and the marsh creeks. The monthly differences of instantaneous feeding ration ($\Delta\%Ir$) between flood and ebb enabled us to estimate the minimal quantity of material swallowed only in the creeks at each tide (see Laffaille *et al.*, 1998). A rapid food intake and maintenance of a constant stomach content during digestion favours a high assimilation of food (Godin, 1981), and may cause the $\Delta\%Ir$ observed in the salt marsh for mullet to be underestimated (see Laffaille *et al.*, 2001).

Adapted from Almeida *et al.* (1993), a 200 mg sample was removed monthly from three mullets' stomachs caught during ebb, and suspended in 5 ml of distilled water. The samples were shaken thoroughly and a known volume was pipetted onto a slide with an etched grid. A constant area was examined in all samples and the food items were identified and counted, for established numeric composition (%N). The frequency of occurrence (%FO) of each food item was estimated according to Hureau (1970) and was classified into three categories (I): accidental, $\%FO < 10\%$; secondary $10\% < \%FO < 50\%$; and preferential $\%FO > 50\%$. The objective was to search for characteristic salt marsh food items in the mullets' stomach contents.

Percentage of organic matter

The percentage of particulate organic matter (%POM) was assessed each month in five stomach contents of mullets caught during ebb according to Almeida *et al.* (1993): $\%POM = [1 - (SWC/SWD)] \times 100$, where SWC is the stomach content weight after ignition (at 480 °C during 48 h) and SWD is the stomach content weight after desiccation (at 50 °C during 48 h).

Statistics

The variations of %Ir and %POM were analysed using ANCOVA (covariate: mullet size; factors: tidal

situation and sampling date) and Tukey's multiple range test accordingly with Sokal and Rohlf (1981). In order to normalize the distribution, an arcsine square root transformation was realized.

Results

A total of 733 *Liza ramada* (>100 mm) specimens were caught between March and November. None occurred during winter sampling (January, February and December), which suggests that they do not colonize salt marshes during the cold season. Of the 416 stomach contents analysed, 85 were from fish caught during flood and 331 during ebb.

The interaction effects of tide situation and sampling date is significant for the instantaneous feeding ration (%Ir) [ANCOVA (factors=tide*date), $df=8$, $F=6.608$, $P<0.001$]. %Ir increase between flood and ebb, from $7.0\% \pm 2.4$ to $14.8\% \pm 3.8$ respectively (Figure 2). At each tide, the mullets thus swallowed a quantity of sediment in the creeks representing at least 7.8% of their body weight. For most sampling months, %Ir is significantly higher at ebb than at flood, suggesting that mullets forage actively every time they invade the tidal creeks. However, the minimal quantity of ingested food varies according to the month, from minimum value (3.2%) in November to maximum value (12.7%) in June. No size dependent variations were found [ANCOVA (covariate=mullet size), $df=1$, $F=1.441$, $P=0.231$].

The stomach content of mullets is mainly composed of sediments, microphytobenthos, a mixture of halophytic and microphytic detritus, and meiofauna (Table 1). Indeed diatoms, copepods, nematodes and detritus are the preferential items ($\%FO > 50\%$). Numerically, diatoms are highly dominant ($\%N > 90\%$) particularly *Gyrosigma accuminatum* and *Paralia sulcata* ($\%N=57\%$). The dominant diatom species are mainly benthic forms (Peragallo & Peragallo, 1897; Hustedt, 1927–1930; Hustedt, 1931–1959; Hustedt, 1961–1966; Hendey, 1964; Germain, 1981; Round *et al.*, 1990; Tomas, 1997) as for other items (zoobenthos and organic detritus).

On average, the stomach contents of *Liza ramada* include $31.3\% \pm 7.6$ of particulate organic matter (Figure 3). As for %Ir, %POM is a monthly variable, which is independent from mullet size [ANCOVA (factor=date), $df=8$, $F=12.361$, $P<0.001$; (covariate=mullet size), $df=1$, $F=0.180$, $P=0.674$]. Two groups are distinguished (Tukey's multiple range test), the first concerns months with the lowest %POM content from March to August ($\%POM=25.7\%$ to 31.7%), the second concerns

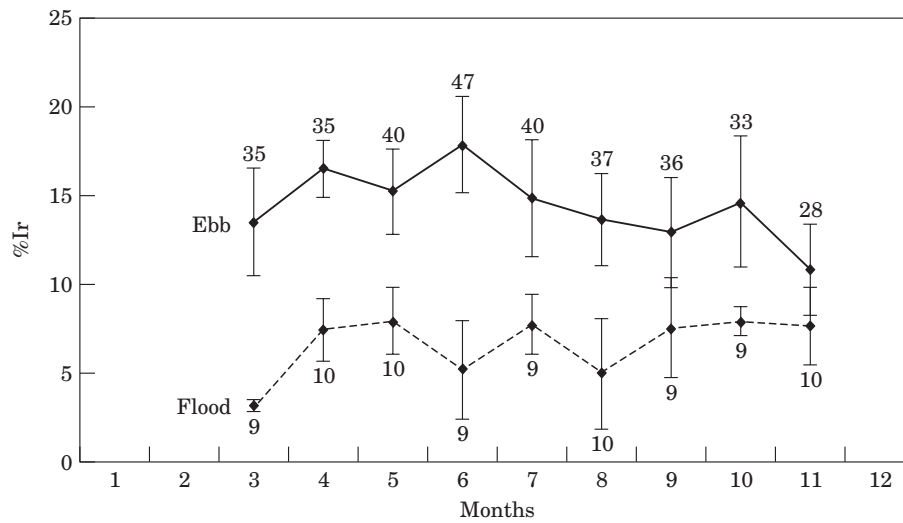


FIGURE 2. Comparison, between ebb and flood tide, of the monthly fluctuations of instantaneous ration (%Ir). Vertical lines represent the standard deviation (sd). Number of stomachs analysed was above or below each standard deviation bar.

TABLE 1. Preferential food items (%FO>50%) identified in the stomach contents of *Liza ramada* caught during ebb tide

Species	%FO	%N	Benthic	Planktonic
Nematods	76.5	6.3	*	
Copepods	76.5	1.0	*	
Diatoms				
<i>Paralia sulcata</i> Ehrenberg	100.0	19.8	*	
<i>Coscinodiscus eccentricus</i> Ehrenberg	100.0	0.8	*	
<i>Actinopterychus senarius</i> Ehrenberg	94.1	2.2	*	
<i>Melosira westii</i> Wm. Smith	94.1	1.8	*	*
<i>Gyrosigma accuminatum</i> (Kutzing) Rabenhorst	82.4	37.1	*	
<i>Navicula</i> sp. (Bory)	82.4	6.2		
<i>Petrodictyon gemma</i> (Ehrenberg) Ehrenberg	82.4	0.4	*	*
<i>Navicula phyllepta</i> Kutzing	76.5	9.8	*	*
<i>Pleurosigma angulatum</i> (Quekett) Wm. Smith	76.5	0.7	*	
<i>Raphoneis amphioceros</i> (Ehrenberg) Ehrenberg	76.5	0.3	*	
<i>Dimeregramma minor</i> (Gregory) Ralphs	58.8	1.4	*	
<i>Brockmanniella brockmannii</i> (Hustedt) Hasle & al.	52.9	4.3	*	*
<i>Odontella aurita</i> (Lyngbye) Agardh	52.9	0.6	*	*
<i>Psammodictyon panduriforme</i> (Gregory) D. G. Mann	52.9	0.3	*	*
<i>Pleurosigma aestuarii</i> (de Brébisson ex Kutzing) Wm. Smith	52.9	0.2	*	*
Indetermined	100.0	4.4		
Detritus	100.0	?	*	

%FO: frequency of occurrence; %N: numerical structure; ?: no data. Round *et al.* (1990) diatom classification. Secondary food items (10%<%FO<50%): *Surirella robusta* var. *splendida* (Ehrenberg) Van Heurck, *Odontella mobiliensis* (Bailey) Grunow, *Surirella ovata* Kutzing, *Lyrella clavata* (Gregory) D. G. Mann, *Podosira stelliger* (Bailey) Mann, *Petroneis humerosa* (de Brebisson) A. J. Stickle & D. G. Mann, *Lyrella hennedyi* (Wm. Smith) A. J. Stickle & D. G. Mann, *Scolioneis tumida* (de Brébisson ex Kutzing) D. G. Mann, *Diploneis crabo* Ehrenberg, *Surirella elegans* Ehrenberg, *Nitzschia lanceolata* Wm. Smith, *Triceratium alternans* Bailey, *Campylosira grevillei* (Wm. Schmidt) Grunow ex Van Heurck, *Grammatophora serpentina* Ehrenberg, *Melosira juergensii* Agardh, *Auliscus sculptus* (Wm. Smith) Ralphs, *Diploneis smithii* (de Brébisson) Cleve, *Grammatophora marina* (Lyngbye) Kutzing, *Odontella rhombus* (Ehrenberg) Kutzing, *Triceratium favius* Ehrenberg & *Amphora* sp. (Ehrenberg ex Kutzing).

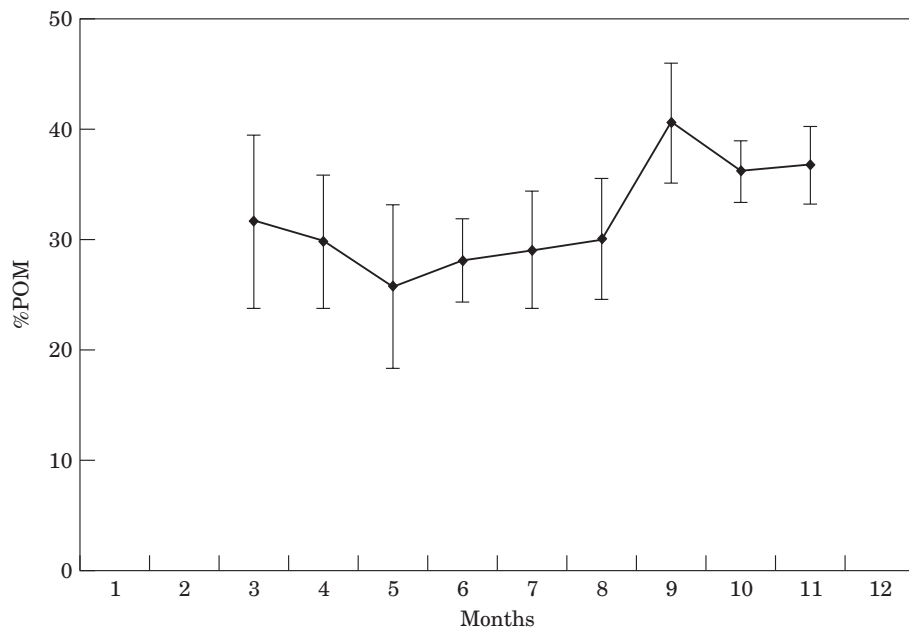


FIGURE 3. Monthly fluctuations of percentage of particulate organic matter (%POM) in stomach contents. Vertical lines represent the standard deviation (sd). Each month, 5 stomach contents were analysed.

autumn (September to November) when %POM is higher (36.1% to 40.5%).

Discussion

Liza ramada is a highly euryhaline species that colonizes the tidal salt marsh creeks of Mont Saint-Michel bay from March to November (Laffaille *et al.*, 2000a). The high %Ir recorded at flood indicates that these fish start foraging the surface of the sediment as soon as (and/or even before) they arrive in the creeks of the salt marsh. The instantaneous feeding ration increases greatly during the 1 to 2 h that the fishes are present in the salt marsh from their arrival in the marsh at flood (on average, %Ir=7%) and their exit at ebb (on average, %Ir=15%). Consequently, we assume that mullet ingest a quantity of sediment representing more than 8% of their body weight during their residence in the salt marsh creeks. This high feeding rate must be related to the site. Indeed, in brackish tidal areas, *L. ramada* feeds mainly at high tide (Almeida *et al.*, 1993) in areas which are only accessible at spring tides (e.g. in salt marsh creek of Mont Saint Michel's bay during 43% of the tides) and for very brief moments (1 to 2 h in these creeks).

Most frequent and dominant items (diatoms, meiofauna and halophytic detritus) have a benthic origin and occur in creek sediments (Lang, 1999; Radureau *et al.*, 1999; Sagan *et al.*, 2000). *Paralia sulcata* is the most widespread diatom in the tidal flats and in the

creeks, therefore it logically occurred frequently in the mullets' stomach contents. Other diatoms such as *Coscinodiscus eccentricus*, *Melosira westii* and *Raphoneis amphiceros* are present either in mudflats or in creeks, whereas *Gyrosigma accuminatum*, *Navicula phyllepta*, *Petrodictyon gemma* and *Pleurosigma angulatum* mainly occur in the creeks (see preceding references) and represent food items characteristic to salt marshes. This confirms that mullet was feeding in the salt marsh creek. Thus we assume that large *Liza ramada* forage in the superficial sediment layer of European macrotidal salt marsh creek, as is the case in other environments (Hickling, 1970; Bruslé, 1981; Almeida *et al.*, 1993; Shapiro, 1998) and for many other mullet species (Odum, 1970; Fagade & Olaniyan, 1973; Masson & Marais, 1975). This interpretation is confirmed by many foraging marks, which are observed on the sediments in the creeks after the ebb. Marchand (1978) and Almeida (pers. comm.) also describe similar foraging marks on the estuary tidal flats sediment of river Loire (France) and River Mira (Portugal), respectively.

The tidal flats are unvegetated and primary production is exclusively due to microphytobenthos communities dominated by diatoms. In the salt marsh (dominated by *Atriplex portulacoides*) of the Mont Saint-Michel bay, less than 1% of halophytic production is exported from salt marshes to intertidal mudflats as macrodetritus (Lefeuvre *et al.*, 2000). Furthermore, fast decomposition processes are

observed on marsh and creek surface sediment: under favourable conditions, the halophytic detritus biomass could disappear in 30 days, due to the high bacterial activity (Créach *et al.*, 1997). This organic matter is rapidly decomposed as nutrients in dissolved organic matter on the production site (Bouchard *et al.*, 1998; Lefeuvre *et al.*, 2000). These nutrients may favour the development of microphytobenthos and mainly diatoms in salt marsh creeks. Both organic matter sources (halophytic detritus in decomposition and microphytobenthos) provide food for limno-benthofagous species such as the mullet *L. ramada* that colonize the salt marsh creek with the flood. Consequently, *L. ramada* directly exploits primary (corresponding to diatoms) and detritic production of macrotidal salt marshes, which are concentrated in the creeks.

The percentage of organic matter contained in the stomach contents is highly variable (between 26% and 40%). Generally, %POM also varies according to the season (Lasserre *et al.*, 1977 for *Chelon labrosus*; Almeida *et al.*, 1993 for *L. ramada*; Cardona, 1999 for *L. saliens*; this study, for *L. ramada*), whereas Hickling (1970) does not report seasonal variation for *L. ramada*. During our study, %POM was maximal in autumn. These monthly variations are likely to be overruled by algae community dynamics (Savouré & Radureau, 1996; Radureau *et al.*, 1999; Sagan *et al.*, 2000) and halophyte detritus in the sediment (Bouchard, pers. comm.). Indeed, diatom densities peak at the beginning of summer and in autumn in the salt marsh creeks. Also the detritus from halophytic plant senescence are maximal in autumn. Moreover, the taste buds of mullets which occur on the mouth-pharyngeal filter (Hossler & Merchant, 1983) enable the selection of highly energetic detritus, but they probably also enable the fish to find the patches where most the abundant and appetising items are present (Larson & Shanks, 1996). This present study confirms that halophyte detritus of salt marsh and benthic microalgae contribute to coastal fishery yield such as demonstrated Peters and Schaaf (1991) and Mallin *et al.* (1992).

Conclusion

Thanks to their important ecological tolerance, mullets may invade tidal creeks where important food resources are available. Despite very short submersion periods, mullets filter and ingest large quantities of sediment, and concentrate and assimilate organic matter produced by these coastal wetlands, which therefore act as important feeding areas for these species and other exploiting fish species (Laffaille *et al.*, 2001). Although organic matter exportation

from salt marshes to sea water by physical vectors such as tidal currents can be significant (Teal, 1962; Nixon, 1980; Gordon & Cranford, 1994), export of organic matter from salt marshes is facilitated by trophic migration of aquatic fauna (Kneib & Stiven, 1982; Kneib, 1987; Lefeuvre *et al.*, 1999). Only a few fish species are able to assimilate salt marsh primary production directly; which is the case for the clupeid *Brevoortia patronus* in the United States (Deegan *et al.*, 1990) and *Liza* spp. in Europe. More than all the other teleosts dwelling in estuaries in temperate areas, mullets probably contribute significantly to the ecological functioning of these systems because they directly use the primary production, they accelerate turnover of microalgae communities and they are involved in energy fluxes in and between coastal marine systems (Odum, 1970; Laffaille *et al.*, 1998; Lefeuvre *et al.*, 1999).

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